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Whoever their partner, female blue tits breed the same.

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Abstract

Do females modify their reproductive investment if they do not succeed to pair with a male that matches their preference? In a two-year experiment, we asked female blue tits (*Cyanistes caeruleus*) to select among six males, and then successively paired them with their preferred and their most avoided male. We monitored female reproductive investment through nest building activity, timing of breeding, size and number of eggs, number of fertilised eggs, and brood sex-ratio. We found that females preferred males with a chromatic coloration (blue UV chroma of the head crown) that matched their own, but also that they preferred males with a lower achromatic coloration (less bright color of the cheeks and head crown). Although females paired with their preferred males tended to build heavier nests during the breeding season, we found no evidence for an effect of the pairing treatment on timing of breeding, or any other aspects of female reproductive investment. We however found that laying dates, clutch sizes, egg sizes and brood sex-ratio were significantly repeatable within females between the two years, despite the opposite pairing treatments. These findings show that in female blue tits, the males with which they are paired do not substantially alter their reproductive decisions.

Keywords: reproduction; mate preference; birds; laying date; clutch size

Introduction

Mate choice is a major component of sexual selection in the animal kingdom (Andersson 1994; Cotton et al. 2006; Höner et al. 2007; Locatello et al. 2015). Individuals can derive benefits for themselves in the present generation, or for their offspring in the following generation, from carefully choosing a mate (Andersson and Simmons 2006; Jones and Ratterman 2009; Kokko et al. 2003). They can consequently be expected to evaluate traits indicating partner condition, characteristics and quality. Animals might use physical characteristics to select their mate, like coloration (Baube et al. 1995; Rowland et al. 1995; Pryke and Griffith 2007; Gomez et al. 2010) or size (McKaye 1986; Howard et al. 1998; Shine et al. 2001; Romero-Pujante et al. 2002; Hoefler 2007). They can also use behavioral traits such as song characteristics (Searcy 1992; Wagner and Reiser 2000; Byers and Kroodsma 2009; Riebel 2009; Caro et al. 2010; Iglesias and Hasson 2017), courtship behaviors (Zuk et al. 1990; Sargent et al. 1998; Kallman et al. 2015; Ota et al. 2015), personality (van Oers et al. 2008; Schuett et al. 2011; Bierbach et al. 2015; Chen et al. 2018; Delaitre et al. 2023) or cognitive abilities (Boogert et al. 2011; Kavaliers and Choleris 2017). Even the chooser's own phenotype, such as its condition, coloration or size (Hunt et al. 2005; Holveck and Riebel 2010; Riebel et al. 2010; Rueger et al. 2016; Caro et al. 2021), can play a decisive role at the time they decide with whom to mate. All those criteria can be used separately or in combination (Burley 1981a; Candolin 2003).

Females, historically considered the choosing sex (Jones and Ratterman 2009; Davies et al. 2012), were initially assumed to reach a consensus about who is the most attractive male, and inter-individual variation in female preference and in the optimal male phenotype were therefore expected to be low (Real 1990; Jennions and Petrie 1997). However, in some species, mating preferences seem largely individual-specific, suggesting that they might rather target genetic or behavioral compatibility (Jennions and Petrie 1997; Widemo and Sæther 1999; Brooks and Endler 2001; Forstmeier and Birkhead 2004; Cotton et al. 2006; Rosenthal and Ryan 2022).

Beyond the difficulty of understanding mate selection processes and targets, the impact of partner selection on female reproductive timing, investment, and physiology is also not easy to predict (Burley 1988; Frank 1990; Penn and Potts 1999; Mays and Hill 2004; Gowaty et al. 2007; Bolund et al. 2009). Two main, non-mutually exclusive hypotheses have been proposed to explain why females would invest differently depending on their preference for their partner.

First, the differential allocation hypothesis states that an individual adjusts its investment in its current reproductive effort according to the perceived attractiveness, or overall quality of its partner (Burley 1986; Burley 1988; Sheldon 2000; Haaland et al. 2017). A higher number of offspring and of higher quality are consequently expected when females are paired with a male of higher perceived quality (De Lope and Moller 1993; Gil et al. 1999; Cunningham and Russel 2000; Gowaty et al. 2003; Limbourg et al. 2004; Velando et al. 2006; Anderson et al. 2007; Gowaty et al. 2007; Walling et al. 2010). For example, female zebra finches lay on average 0.5 eggs more when paired with their preferred males, which produce songs of longer duration and faster rate, and are consequently considered higher quality males (Balzer and Williams 1998). In mallards (*Anas platyrhynchos*), females mated with a less-preferred male produce smaller eggs and therefore lower quality offspring (Cunningham and Russel 2000; Bluhm and Gowaty 2004).

Second, the sex-allocation theory predicts that, when the fitness of sons and daughters differs, parents should adjust the sex-ratio of their brood (Charnov 1983; Frank 1990; Booksmythe et al. 2017). Consequently, when sons inherit from their fathers some traits that determine their own attractiveness, females are expected to adjust their brood sex-ratio depending on the qualities of the male with which they are paired (Burley 1981b; Burley 1986; Hardy 2002; Saino et al. 2002; West and Sheldon 2002; Sato and Karino 2010; Bowers et al. 2013; Booksmythe et al. 2017). Females are therefore predicted to produce more sons when mated to a male of higher quality. Great tit (*Parus major*) females have for example been suggested to produce more sons when they are paired to larger males (Kölliker et al. 1999).

Studies investigating the traits used in mate choice and its consequences on reproductive investment have usually been conducted in the wild (Bonneaud et al. 2006; Foerster et al. 2006; Eriksen et al. 2009; García-Navas et al. 2009; Fargevieille et al. 2017). The drawback is that it is often impossible to control, and even know, all the factors that influence mate choice and its subsequent effects on reproduction. The pairings observed in the wild are indeed the result of a series of events mixing mate preferences, competition with other females for males and territories, male availability, and finally mate choice (Jennions and Petrie 1997; Widemo and Sæther 1999; Edward 2015; Scauzillo and Ferkin 2019). Disentangling the respective roles of the different mate choice components may therefore request experiments in controlled conditions, which artificial characteristics may in turn hamper the expression of natural behaviors. In the case of mate preference studies, many have only offered binary choices between two potential partners (Amundsen et al. 1997; Witte et al. 2000; Romero-Pujante et al. 2002; Tomaszycki and Adkins-Regan 2005; Burley and Foster 2006; Rutstein et al. 2007;

Reparaz et al. 2014; Kniel et al. 2015; Caro et al. 2021), or have only manipulated one phenotypic trait and not the overall signaling value of an individual (Clayton 1990; Bennett et al. 1996; Waas and Wordsworth 1999; Caro et al. 2021; Cantarero et al. 2022), which may lead to unnatural contrasts among the sexual signals conveyed (Caro et al. 2021).

In the present study, we adopted an intermediate approach mixing the advantages of wild and captive studies, to test the two hypotheses described above. We first investigated mate preferences of blue tits (*Cyanistes caeruleus*) in captivity by offering females the choice between six, unmanipulated, males. In particular, we evaluated whether male body size, personality and color traits explain the preference patterns expressed. We then paired half of the females with their preferred male and the other half with their most avoided one. We conducted this experiment over two years, so that each female was paired with its preferred male in one year and with its most avoided male in the other. Thus, each female acted as her own control. In line with the differential allocation hypothesis and the sex allocation theory, linking reproductive investment to mate preference, we hypothesised that females paired with their favorite male would lay more and larger eggs, and would produce more fertilised eggs (differential allocation hypothesis), and more sons (sex allocation theory). In addition, we also hypothesised that females paired with their favorite male would build heavier nests and lay earlier in the season. Indeed, nest-building activities of females are stimulated by the presence of a male (Hinde and Steel 1976), and males can stimulate female gonadal development and hormone secretions through social interactions (Erickson and Lehrman 1964; Hinde and Steel 1976; Hinde and Steel 1978; Silverin and Westin 1995; Stevenson et al. 2008; Perfito et al. 2015), which can result in earlier laying (Adkins-Regan and Tomaszycki 2007; Griffith et al. 2011; Crino et al. 2017; Delaitre et al. 2023).

Methods

Ethical note

Blue tits were trapped and maintained under licenses 2018-s-11 issued by the Direction Régionale de l'Environnement, de l'Aménagement et du Logement Languedoc-Rousillon; and 15-XIX-116 issued by the Direction Départementale de la Protection des Populations de l'Hérault. Experiments were run under the license 2017-XIX-075 from the Direction Départementale de la Protection des Populations de l'Hérault, and approved by the Ethical committee N°036 with reference APAFIS#2021120712067677 #34249 v2.

Birds and general procedures

Blue tits originated from the long-term studied population of La Rouvière (43.621°, 3.733°) at Montarnaud near Montpellier. They were born in the wild in 2019, collected as chicks (10 days old) in nest-boxes, and subsequently hand-raised in captivity until independence (35 days old), following the procedure described in Reparaz et al. (2014) and Caro et al. (2021). Birds were kept in large outdoor aviaries (27 m³) as standard housing. They were fed with cake made of sunflower seed grease, eggs, sugar, wheat flour and high-protein pellets (Show 1+2 crumble, Versele-Laga, Deinze, Belgium), supplemented with minerals, vitamins, amino-acids and carotenoids (Nutribird A21, Versele-Laga, Deinze, Belgium; Nekton-S, Günter Enderle, Pforzheim, Germany; Yel-Lux, Versele-Laga, Deinze, Belgium) and mealworms. Food and water were provided *ad libitum*.

Preference test

Experimental subjects and housing

The experiment took place at the CEFÉ in Montpellier, France, for two consecutive years. We used 24 female and 29 male blue tits the first year and 23 females and 23 males the second year. All birds used in the second year had already been used the first one, in such a way that each female acted as its own control (see below). Birds were moved from aviaries to individual cages (0.8 x 0.4 x 0.35 m) on 8th December 2020 and on 11th January 2022, across 3 indoor rooms. Females and males were housed in separate rooms. Windows in rooms allowed birds to be exposed to natural light, and supplementary artificial lightning was provided from 15min after natural sunrise until 15 min before sunset to respect the natural increase and decrease of light intensity every day. Windows were left open to expose birds to natural fluctuations of temperature.

Experimental setup

Females were tested in a carousel-shaped six-choice chamber inspired by Zandberg et al. (2017) (figure 1, figure S1) from 12th to 21st December 2020 for the first year and from 19th to 24th February 2022 for the second year. We ran the preference tests a bit later in 2022 compared to 2021 in order to be a bit closer to breeding. All tests took place in a test room (4.0 x 2.4 x 2.5 m) with white walls, and high-frequency fluorescent lights. In the six-choice setup, each female could see all stimulus male birds from the central platform, but when in the choice zone of a stimulus male, she could not see the other males (figure 1). The males were visually isolated from each other. Before being tested, each female was given 15 min to habituate to this

new environment. In the meantime, the six stimulus males were transferred from their home cage to six individual mobile cages (47 x 28 x 26 cm) in an adjacent room. At the end of the 15 min habituation period, each male cage was placed into one of the six compartments of the carousel. Each female was tested once with one group of six stimulus males during 90 minutes. The experimenter left the room at the beginning of the test, which was video-recorded using three GoPro cameras (GoPro, Inc., USA) affixed above the test chamber. After each test, all birds were returned to their individual home cages. Videos were analysed soon after the end of each test and, depending on the treatment to which the female was assigned for the breeding experiment (see below), the male with which she spent the most time (hereafter called the preferred male) or the lowest amount of time (hereafter called avoided), was pulled out of the pool of available males for the next females to be tested. Stimulus males could not belong to the family of the female tested and their positions in the setup were randomised for each test.

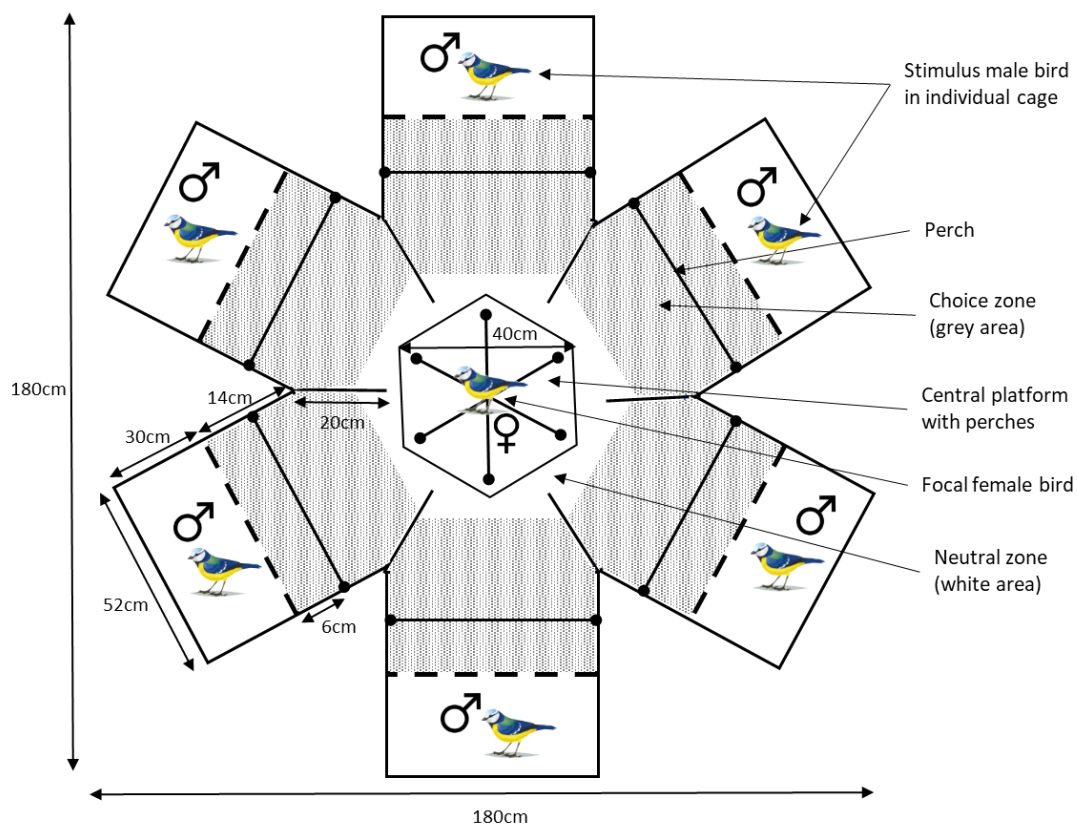


Figure 1. Experimental mate preference test setup. Females were tested for their preference in a six-choice setup for 90 min. From the hexagonal central platform, the focal female could observe all stimulus male birds, whereas only one stimulus male was visible from the perch in the choice zone. The stimulus male birds could not see each other. Time spent in the choice zone of each male was inferred as a proxy for preference. At the end of each test, videos were analysed and, depending on the treatment assigned to the female, the preferred (or avoided) male was pulled out of the pool of available males for the next females tested. Positions of the stimulus male birds were randomised for each test.

Video analysis

Videos were analysed using Behavioral Observation Research Interactive Software (BORIS) (Friard and Gamba 2016) version 7.9.7–14/01/2020 (<https://www.boris.unito.it/>). The time spent by the females in the choice zone of each stimulus male bird was extracted from each video, and used as a proxy for mate-choice (Gonçalves and Oliveira 2003; Witte 2006). All females visited the choice zone of each male at least once during the 90 min of the test. Neither the males nor the females showed any clear solicitation of mating behavior. The time spent by the female in the choice zone of the male was consequently the most appropriate and direct method for estimating female preference.

Phenotypic trait measurements

To identify on which criteria females choose their mate, a set of phenotypic traits was measured on each male and female tested, ahead of the preference tests each year. We measured an achromatic trait, brightness (i.e. the area under the reflectance curve divided by the width of the interval from 300–700 nm, and that can be defined as the total amount of light reflected from the measured surface (Saks et al. 2003)) for the white of the cheek, the yellow of the breast and the UV-blue of the head crown, and a chromatic trait, chroma (i.e. the proportion of the total reflectance falling in the color range) for UV-blue of the head crown ($R_{300-400} / R_{300-700}$) and yellow of the breast ($R_{\max\ 500-700} - R_{450} / R_{300-700}$) (Fargevieille et al. 2017). Higher UV-chroma values correspond to a stronger UV signal, and higher yellow chroma values are associated with higher levels of carotenoids in the plumage (Isaksson et al. 2008). We measured coloration of each bird with a spectrophotometer (AVASPEC 2048, Avantes, Apeldoorn, the Netherlands) equipped with an AVALIGHT-DHS deuterium-halogen lamp (Avantes, Apeldoorn, the Netherlands) and a 200 μm optical probe (FCR-7UV200-2-45-ME, Avantes, Apeldoorn, the Netherlands) whose tip contained a 45° quartz window. Reflectance was calculated in relative terms, via comparison with a black and a white reference (WS1, Ocean Optics, Dunedin FL, USA). We also took morphological measures, including body mass, tarsus, beak and wing lengths. Ahead of the present study, a personality score was derived from exploratory behavior trials in a novel environment, following the protocol described in Charmantier et al (2017) and Dubuc-Messier et al (2017). Briefly, each bird was released separately in a novel environment, which consisted of an exploration cage equipped with 2 perches (0.6 \times 0.4 \times 0.4 m). Once the bird entered the cage, its movements were observed for five minutes. Birds were given an exploration score on a continuous scale based on the total number of movements between the perches, as well as hops up and down and flights. Scores

ranged from 47.5 to 260.5, with higher scores indicating faster exploration, and lower scores indicating slower exploration. This kind of measurement has been used to measure exploration behavior in great tits (Stuber et al. 2013) and blue tits (Mutzel et al. 2013; Charmantier et al. 2017; Dubuc-Messier et al. 2017), and provides repeatable exploratory scores (Dingemanse et al. 2002; Stuber et al. 2013).

Breeding experiment

Pair formation and housing of birds

Before the first preference test, females were randomly distributed across two groups: 12 females paired with the male with which they spent the most time and 12 (11 in 2022) females paired with the male they avoided most. On the second year, we reversed the groups, i.e. a female that had been paired with its preferred male the first year, was paired with its most avoided male the second year. That way each female was used as its own control. Females and males were released simultaneously in outdoor aviaries (2.5 x 3 x 3 m). Pairs were moved in aviaries on 4th January 2021 and on 28th February 2022. Nesting materials consisting of moss and dog, horse and donkey hair were provided from early March.

Reproduction monitoring

Starting from mid-March, we monitored nest building and egg laying activities, first once a week, then twice a week as birds were closer to lay (Dufva 1996). The date the first egg was found was recorded as the pair laying date. Tits usually lay one egg every 24 hours (Perrins 1970), so if more than one egg was found in the nest at the day of checking, we back calculated the laying date. All eggs were measured to the nearest 0.05 mm with a calliper (Ecotone Measy DG), marked with a fine point marker, and replaced in the nest until clutch completion. After at least five days of incubation, nest and eggs were collected, and eggs were candled to identify if an embryo was developing. Eggs were then wiped with paraffin oil and stored at -20°C until further analyses (see below). Nests were dried in an oven at 40°C for 48h and then weighted to the nearest 0.1 g (Precisa, France).

Egg analyses

Germinal disc observation

127 eggs the first year and 177 eggs the second year were collected and preserved in a freezer. Eggs were candled when they were collected, but this method does not enable to distinguish between an unfertilised egg and a fertilised egg in which the embryo died at an early

stage of development. We thus examined the germinal disc (GD) following the method described in Birkhead et al (2008) to identify if an egg was fertilised or not (figure S2). In short, we opened the eggs, discarded the albumen, placed the yolk in a small Petri dish and examined the aspect of the GD under a binocular dissecting microscope (Optika, Italy). Photos of the observed GD was taken with a camera (OPTIKA C-B5), and the OPTIKA PROview software (version x64, 4.11.18914.20210510, <https://www.optikamicroscopes.com/optikamicroscopes/>).

Embryo sexing

107 out of the 127 eggs collected the first year and 117 out of the 177 eggs collected the second year contained an embryo and we succeeded to sex 105 and 114 of those embryos the first and second year, respectively. We sampled between 5 and 20 mg of embryo tissue and extracted the DNA using the DNeasy Blood & Tissue Kit (Ref 69506, QIAGEN). DNA extraction products were analysed by agarose gel electrophoresis (1% in TBE) and visualized under UV light after staining with ethidium bromide, using a molecular size marker of a 1 kb Plus “ladder” type (Quick-Load, N0469S, New England BioLabs Inc.). The sex identification test employs the P8 (5'-CTCCCAAGGATGAGRAAYTG-3') and P2 (5'-TCTGCATCGCTAAATCCTTT-3') primers (Griffiths et al. 1998) and PCR amplification was carried out in a total volume of 20 μ L. For each individual, reaction conditions were as follows: 1 μ L Buffer 10X (Eurogentec, Belgium); 1.5 μ L MgCl₂ 25mM; 1 μ L dNTP Master mix 20mM total (Eurogentec, Belgium); 1 μ L P2 10 μ M (Eurogentec, Belgium); 1 μ L P8 10 μ M (Eurogentec, Belgium); 0.2 μ L 0.15 units of Red diamond Taq DNA polymerase (Eurogentec, Belgium), 12.3 μ L H₂O; 1 μ L DNA. PCR was performed in a thermal cycler (Eppendorf AG, Hamburg, Germany). An initial denaturing step at 94 °C for 5 min was followed by 30 cycles of 48 °C for 45 s, 72 °C for 45 s and 94 °C for 30 s. A final run of 48 °C for 1 min and 72 °C for 5 min completed the program. PCR products were analysed by agarose gel electrophoresis (3% in TBE) and visualized under UV light after staining with ethidium bromide, using a molecular size marker of a 100 bp “ladder” type (Quick-Load, N0467S, New England BioLabs Inc., USA).

Statistical analyses

All the analyses were performed in R version 4.2.2 (R Core Team 2022). Linear mixed-effects models and generalized linear mixed-effect models were conducted using the lme4 version 1.1.31 (Bates et al. 2015) and glmmTMB version 1.1.5 (Brooks et al. 2017) packages. P-values were obtained with the lmerTest package version 3.1.3 in the case of mixed-model

analyses (Kuznetsova et al. 2017). Plots were created with the ggplot2 version 3.4.0 (Wickham 2016) and ggeffects version 1.1.5 (Lüdtke 2018) packages. Models were simplified using backward elimination of the nonsignificant terms, starting with the higher-order interactions (Crawley 2007), we set $\alpha=0.05$. Correlations were calculated and plotted with the Hmisc version 4.7.2 (Harrell 2022) and corrplot version 0.92 (Wei et al. 2017) packages, respectively. Principal component analyses were run with FactoMineR version 2.7 (Husson et al. 2016) and factoextra version 1.0.7 (Alboukadel and Mundt 2017) packages. Repeatability was measured using the rptR package version 0.9.22 (Stoffel et al. 2017).

Preference test

We ran a linear mixed-effect model with the time (in seconds) spent by the female in the choice zone of each male as response variable. Explanatory variables consisted of each male trait, alone and in interaction with the female corresponding trait. These included brightness (white of the cheek, yellow of the breast, UV-blue of the head crown), chroma (yellow and UV-blue), body mass, tarsus, wing and beak size and exploration score. As we had an important number of variables on a relatively restricted number of individuals, we first checked correlations between variables (figure S3). Principal Component (PC) were used for body size to decrease the number of variables to add in the model. It included body weight and tarsus and wing length (figure S4). Identification of the female and year were added as crossed random intercepts, to account for the fact that each female occurred six times in the dataset (once for each six different males) and that females were used in both years of experiment. The response variable (i.e. the time spent in the choice zone of the males) was weighted by the “interest” of the female to allow more statistical weight to the females that spent more time evaluating the males during the test rather than staying in the neutral zone (Reparaz et al. 2014; Caro et al. 2021). “Interest” thus depicts the overall motivation of the female to visit the males during the experiment by indicating the proportion of time that the female spent close to the six stimulus males (i.e. not in the central neutral zone), and was calculated as follows (Reparaz et al. 2014; Caro et al. 2021) :

$$\text{Interest} = \frac{\text{Time spent with (male 1 + male 2 + male 3 + male 4 + male 5 + male 6)}}{\text{Total duration of the test (90min)}}$$

Breeding experiment

Out of the 47 pairs that were formed across both years, 4 pairs had to be removed from the statistical analyses (because a member of the pairs died or was injured before or during the experiment), we thus analysed the reproductive behavior of 43 pairs.

We first used binomial tests to compare the number of females that (i) built a nest and (ii) laid at least one egg, between females paired with their preferred and avoided male, as well as (iii) the total number of eggs laid by all the females on the whole breeding season between the two groups.

We tested the effect of the pairing treatment on female reproductive parameters. We performed linear mixed-effect models on (i) nest weight, (ii) lay date, (iii) egg measures (PC1, see below) and generalized linear mixed-effect models with Poisson distribution on (iv) clutch size and with binomial distribution on (v) the proportion of fertilised egg and on (vi) the proportion of male chicks produced by each female during the breeding season. PC were used for egg measured because egg length, breadth and volume were correlated. The PC1 axis explained 80.6% of the variability in the data (figure S5). In all models, the treatment (preferred *vs.* avoided) and the year (2021 *vs.* 2022) were included as explanatory variable. Female ID was included as random effect to account for the fact that the same females were used in both years, and that a same female laid several eggs. As 11 females laid on both years, we measured repeatability of the female identity for each model using the rpt function.

Results

Preference test

Females spent more time close to males with a blue UV chroma of the head crown that was similar to their own ($p = 0.036$, Table 1, figure 2A). That's the only phenotypic traits for which females referred to their own phenotype, all the other interactions between male and female characteristics were non-significant (Table 1). Females also spent more time close to males with a duller blue head ($p = 0.007$, Table 1, figure 2B) and tended to prefer males with duller white cheeks ($p = 0.084$, Table 1, figure 2C). We did not find that females were attracted by any other male phenotypic trait, including body size (PCA body size: $p = 0.544$, beak length: $p = 0.707$, Table 1) and exploration score ($p = 0.514$, Table 1).

Table 1. Results from a linear mixed effect model, exploring the variables that influence the time spent by the females in the choice zone of the males during the 90 minutes of the test ($n = 47$ females). Variables in bold had a significant effect on the response variable ($p < 0.05$), italicized variables depict trends ($p < 0.10$). Variables in light grey were removed during the reduction of the model, and presented in the reverse order in which they were removed.

Explanatory variable	Estimate	S.E	df	F value	p-value
Intercept	213.07	77.21			
PCA Body size male	15.74	25.87	124.11	0.37	0.544
Beak length male	11.95	31.75	125.91	0.14	0.707
Exploration score male	13.88	21.21	121.49	0.43	0.514
<i>White brightness male</i>	<i>-48.04</i>	<i>27.62</i>	<i>123.07</i>	<i>3.03</i>	<i>0.084</i>
Blue brightness male	-64.34	23.42	123.12	7.55	0.007
Yellow brightness male	-17.89	29.12	123.22	0.38	0.540
Yellow chroma male	25.18	26.10	122.01	0.93	0.337
Blue UV chroma male	-29.97	34.67	124.15	0.75	0.389
Blue UV chroma female	-8.35	33.37	38.74	0.06	0.804
Blue UV chroma male*Blue UV chroma female	47.86	22.5	118.13	4.51	0.036
Blue brightness female	-10.68	29.22	71.79	0.13	0.716
Blue brightness male*Blue brightness female	10.96	17.51	117.85	0.39	0.533
Exploration score female	-19.70	42.29	18.42	0.22	0.647
Exploration score male*Exploration score female	-17.49	26.96	105.03	0.42	0.518
Beak length female	-38.65	39.77	18.54	0.34	0.344
Beak length male*Beak length female	11.38	25.26	100.09	0.20	0.653
<i>Yellow brightness female</i>	<i>-53.27</i>	<i>29.79</i>	<i>71.49</i>	<i>3.19</i>	<i>0.078</i>
Yellow brightness male*Yellow brightness female	11.75	26.63	103.70	0.19	0.659
Yellow chroma female	-6.77	43.12	28.08	0.02	0.876
Yellow chroma male*Yellow chroma female	4.53	19.27	97.42	0.06	0.815
White brightness female	36.89	42.08	50.88	0.77	0.385
White brightness male*White brightness female	9.23	34.71	98.74	0.07	0.791
PCA Body size female	22.00	49.44	16.51	0.19	0.662
PCA Body size male* PCA Body size female	1.33	21.69	96.29	0.004	0.951

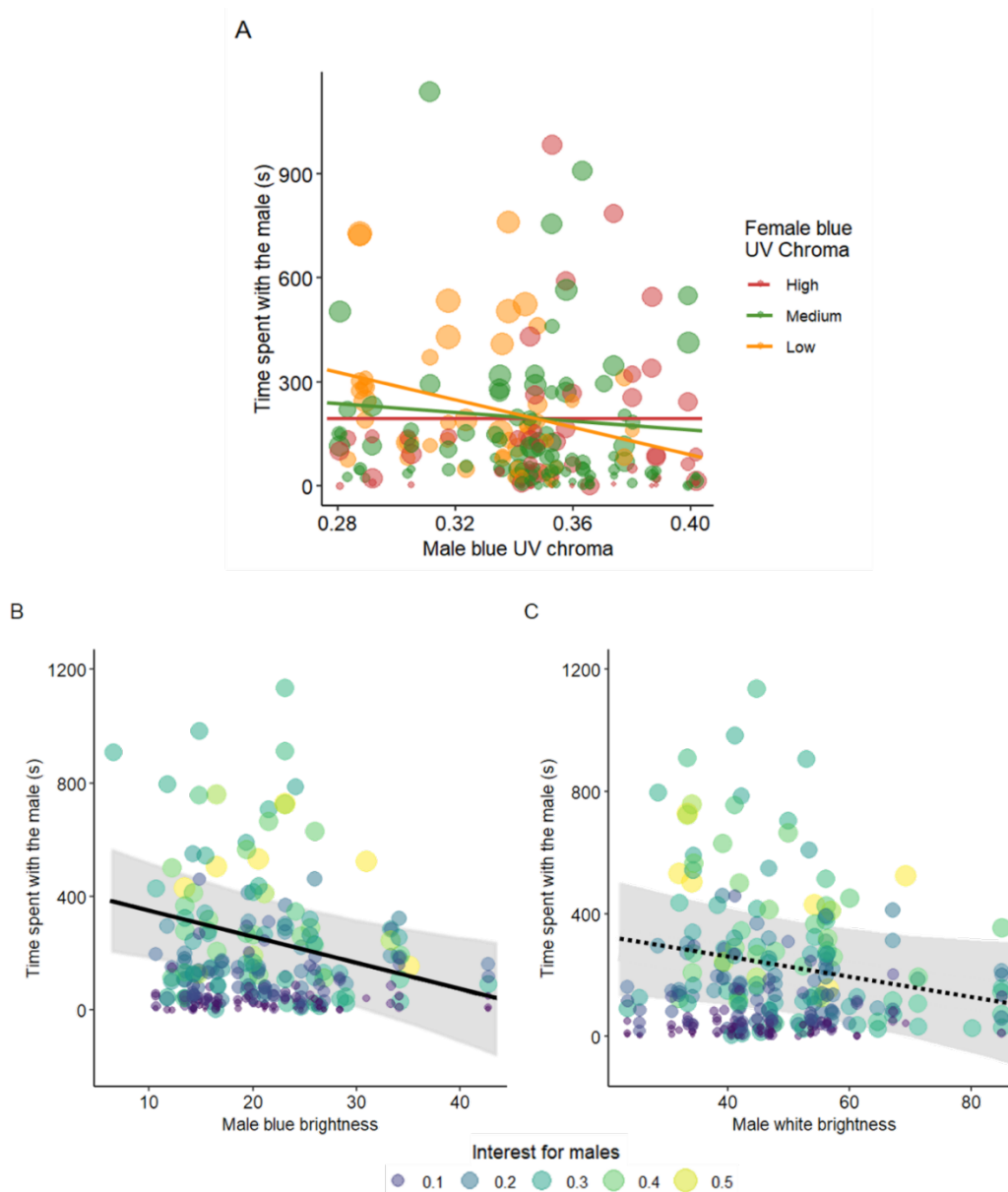


Figure 2. Female preferences for male color traits.

A: Females prefer male with blue UV chroma of the head crown similar to their own ($F_{1,118.13} = 4.51, p = 0.036$). The lines represent the predicted values of the model. Although female blue UV chroma was treated as a continuous variable in the statistical model, for graphical purpose they were split into three categories corresponding to the 25% (i.e. low, orange), 50% (medium, green) and 75% (high, red) quantiles. This graphical representation suggests that the interaction could be mostly driven by females with low blue UV chroma preferring males with low blue UV chroma.

Female blue tits prefer males with duller (B) blue head crown ($F_{1,123.12} = 7.55, p = 0.007$) and (C) tended to prefer males with duller white cheeks ($F_{1,123.07} = 3.03, p = 0.084$). Lines and dotted lines represent the predicted values of the model, with the 95% confidence intervals.

On all graphs, points depict individual data and their size represents the overall interest of females for males, with bigger points depicting a higher interest for males during the preference test.

Breeding experiment

Females built a nest in 36 out of 43 occasions (18 in 2021, 18 in 2022, Table 2), but counts were identical in both treatments (18 in the preferred treatment vs. 18 in the avoided treatment; binomial test, $p = 1$, Table 2). Similarly, the 26 clutch initiations (12 in 2021, 14 in 2022, Table 2) were evenly distributed between the two treatments (13 females in each group; binomial test, $p = 1$, Table 2), and females produced a similar total number of eggs in each treatment (165 eggs in total in the preferred male group vs. 162 eggs in the avoided group, binomial test, $p = 0.91$). However, comparing the total number of eggs between treatments for each year separately, revealed that there were more eggs produced in the preferred than in the avoided group in 2021 ($p = 0.001$, Table 2), while this was the opposite in 2022 ($p = 0.007$, Table 2). As females were exposed to opposite treatments over these two years, this result suggests that it is not the preference for the male that influences the number of eggs laid by the females.

Table 2. Counts of number of nests built, clutch initiations and total number of eggs laid per year and treatment. Each female was used as its own control, i.e. a female that had been paired with its preferred male the first year was paired with its most avoided male the second year. Females laid more eggs in 2021 with the preferred males while they laid more eggs with the avoided one in 2022.

	2021		2022	
	Preferred	Avoided	Preferred	Avoided
Number of nests built	9	9	9	9
Number of females that initiated laying	7	5	6	8
Total number of eggs laid	95	55	70	107

At the individual level, females tended to build heavier nests when paired with their preferred male ($n = 36$, $F_{1,33} = 3.56$, $p = 0.068$, Table 3, figure 3A), but they did not lay earlier ($n = 26$, $F_{1,12.24} = 0.03$, $p = 0.874$, Table 3, figure 3B), nor lay larger clutches ($n = 25$, $z = -0.07$, $p = 0.944$, Table 2, figure 3C). Mean egg size was also similar between groups ($n = 320$, $F_{1,306.78} = 2.23$, $p = 0.137$, Table 3). Finally, we did not find any difference in the proportion of fertilised eggs between the two groups ($n = 282$, $z = -0.03$, $p = 0.977$, Table 3, figure 3D), nor in the proportion of male chicks ($n = 219$, $z = -0.55$, $p = 0.580$, Table 3, figure 3E).

Being paired with a preferred or an avoided male therefore does not seem to make much of a difference in female blue tits. This is further supported by our analyses of the repeatability of the traits we monitored during the breeding season. Laying date ($R = 0.413$, $p = 0.048$, Table 3), clutch size ($R = 0.87$, $p < 0.001$, Table 3), egg size ($R = 0.75$, $p < 0.001$, Table 3) and

proportions of sons ($R = 0.758, p = 0.017$, Table 3) were indeed significantly repeatable within females over the two years of experiment, showing that females are relatively consistent in these decisions, whatever the male with which they are paired. Nest weight and proportions of fertilised eggs were not repeatable (Table 3).

Table 3. Results from generalized linear mixed effect models and linear mixed effect models exploring the variables that influence nest weight, laying date, clutch size, egg size and proportion of fertilised eggs and male chicks. Repeatabilities of female identity have been measured with the rpt function. Bold writing depicts significant results ($p < 0.05$), italicized depicts trends ($p < 0.10$). Est.: Estimate, S.E: Standard Error, R: Repeatability, CI: 95% Confidence Interval.

	Nest weight			Laying date			Clutch size		
<i>Fixed effects</i>	<i>Est.</i>	<i>S.E</i>	<i>p</i>	<i>Est.</i>	<i>S.E</i>	<i>p</i>	<i>Est.</i>	<i>S.E</i>	<i>p</i>
Treatment	2.36	1.25	0.068	0.38	2.32	0.874	-0.01	0.15	0.944
Year	1.91	1.25	0.137	-0.52	2.33	0.828	0.19	0.15	0.191
<i>Repeatability</i>	<i>R</i>	<i>CI</i>	<i>p</i>	<i>R</i>	<i>CI</i>	<i>p</i>	<i>R</i>	<i>CI</i>	<i>p</i>
Female identity	0	0- 0.601	1	0.413	0- 0.87	0.048	0.87	0.657- 0.981	<0.001

	Egg size			Prop. fertilised eggs			Prop. male chicks		
<i>Fixed effects</i>	<i>Est.</i>	<i>S.E</i>	<i>p</i>	<i>Est.</i>	<i>S.E</i>	<i>p</i>	<i>Est.</i>	<i>S.E</i>	<i>p</i>
Treatment	-0.16	0.10	0.137	-0.05	1.59	0.977	-0.50	0.91	0.580
Year	-0.38	0.10	<0.001	0.93	1.62	0.568	-0.29	0.91	0.742
<i>Repeatability</i>	<i>R</i>	<i>CI</i>	<i>p</i>	<i>R</i>	<i>CI</i>	<i>p</i>	<i>R</i>	<i>CI</i>	<i>p</i>
Female identity	0.75	0.564- 0.85	<0.001	0	0- 0.826	1	0.758	0.398- 0.975	0.017

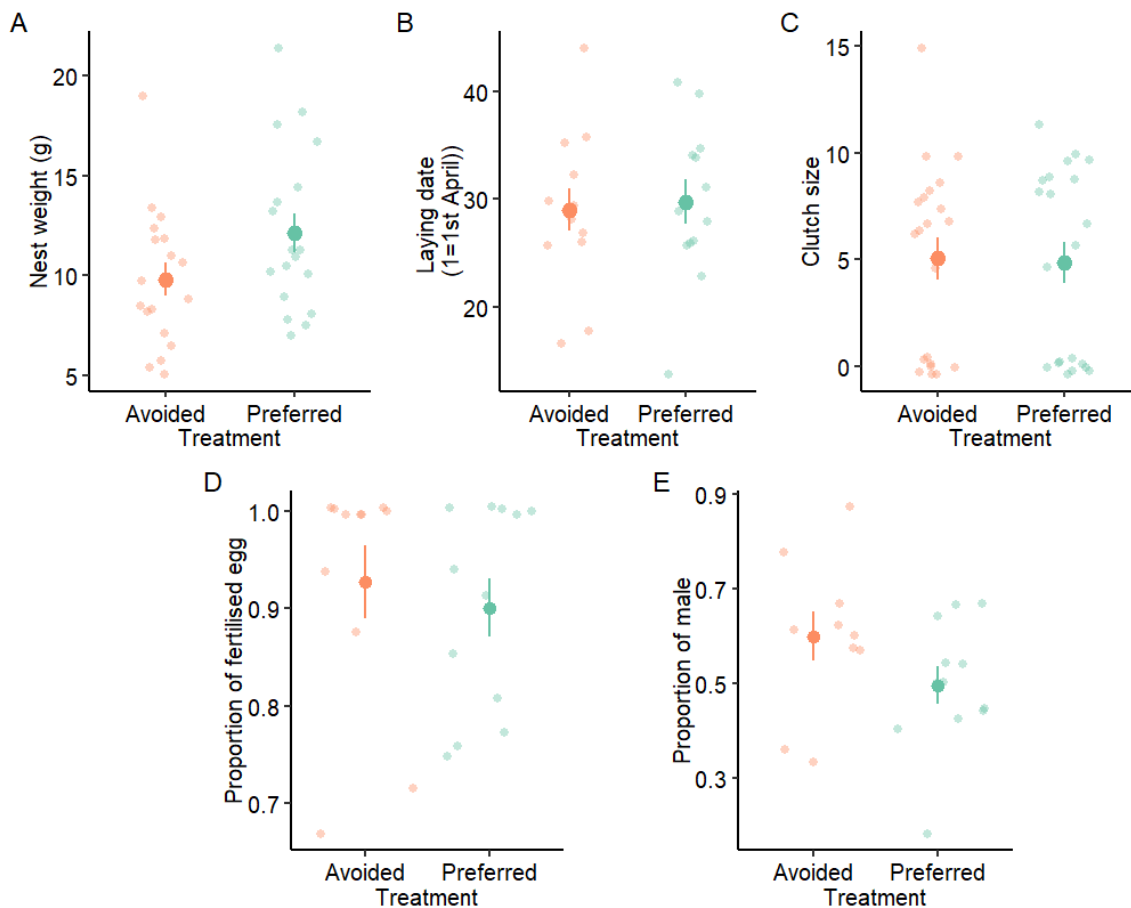


Figure 3. Effect of the preference of the females on their reproductive parameters.

Females tended to build heavier nests when paired with their preferred male ($p = 0.068$; panel A), but they did not lay earlier ($p = 0.874$; panel B) or larger clutches ($p = 0.944$; panel C). They also did not produce more fertilised eggs ($p = 0.977$; panel D) or male chicks ($p = 0.580$; panel E). Large dots and error bars represent mean \pm SE, smaller dots depict raw data.

Discussion

We found assortative preference of female blue tits for blue UV chroma of the head crown, a relationship that might have mostly been driven by females with low blue UV chroma selecting males that also presented low levels of blue UV chroma (figure 2A). We also found that females expressed a general preference for males with duller blue head crown and tended to prefer males with duller white cheeks. Contrary to our hypotheses however, we found no effect of female preference on reproductive timing and investment. Although females paired with their preferred male tended to build heavier nests, they did not lay earlier, more or bigger eggs, and they did not produce more fertilised eggs or more sons, compared to females paired with the male they avoided during the preference test. Females however showed significant

repeatability for laying dates, clutch sizes, egg sizes, and egg sex-ratio, despite the fact that they each had been paired with both their preferred and most avoided males.

A first finding of our experiment is that female blue tits expressed preferences for males that had values of blue UV chroma similar to their own, but at the same time they also preferred males with duller blue heads and tended to prefer males with duller white cheeks. All three signals (blue UV chroma, blue and white brightness) have been suggested to be linked to individual quality (Pärt and Qvarnström 1997; Keyser and Hill 2000; Mennill et al. 2003; Alonso-Alvarez et al. 2004; Ferns and Hinsley 2004; Siefferman and Hill 2005; Delhey et al. 2006; Galván and Sanz 2008; Rémy et al. 2010; Midamegbe et al. 2011; Doutrelant et al. 2020; White 2020). For example, in the blue Grosbeak (*Guiraca caerulea*), blue brightness indicated male ability to hold large territories with more resources (Keyser and Hill 2000), and in the great tit (*Parus major*), males with more immaculate white cheek patches had significantly greater access to feeding sites and produced heavier chicks (Ferns and Hinsley 2004). UV coloration has also been suggested to reflect genetic quality (Brown 1997; Foerster et al. 2003; Kempenaers 2007; García-Navas et al. 2009; Ferrer et al. 2015). Female preference for males with similar blue UV chroma to their own could therefore select a male with the same level of quality than themselves (Jennions and Petrie 1997; Tregenza and Wedell 2000; Cotton et al. 2006). This is in line with several studies showing assortative mating in blue tits in the wild (Andersson et al. 1998; Hunt et al. 1999; Fargevieille et al. 2017). A closer look at figure 2A suggests that it is particularly females with low blue UV chroma that prefer males with low blue UV chroma. In captivity, more colored individuals might be more aggressive (Senar 2006), and pairing with an aggressive partner may lead to reproductive failure (Caro et al. 2007). High blue UV chroma males might therefore be more aggressive toward females. Consequently, females with higher blue UV chroma levels, assumed to be more aggressive, would be less choosy because they would be better able to defend themselves, contrary to low blue UV chroma females, which could explain why low blue UV chroma females seem to express clearer preference than higher blue UV chroma females. Females also surprisingly preferred males with duller, and not brighter, blue heads and white cheeks. Caro et al (2021) also found preference for individuals with paler chest plumage in captive blue tits. Consequently, our females would select duller individuals based on blue and white brightness to avoid aggressive individuals in a restricted environment (Caro et al. 2021).

Surprisingly, besides nests that tended to be bigger with their preferred males, female blue tits did not adjust any other reproductive traits to the male with which they were paired. If

females were to match their reproductive decision to the differential allocation hypothesis (Burley 1986; Burley 1988; Sheldon 2000; Haaland et al. 2017), which predicts that male attractiveness should modulate female reproductive investment (Cunningham and Russel 2000; Gowaty et al. 2003; Limbourg et al. 2004; Anderson et al. 2007; Walling et al. 2010), we expected females to lay earlier, more and larger eggs and more fertilised eggs when paired with their preferred male. For example, female zebra finches and barn swallows (*Hirundo rustica*) paired with an attractive male lay larger clutches (De Lope and Moller 1993; Balzer and Williams 1998), and we recently showed that female great tits lay earlier when they are paired with a male they prefer (Delaitre et al. 2023). None of this happened with our blue tits, which therefore do not seem to match the differential allocation hypothesis. Alternatively, we hypothesized that if females were to match the sex-allocation theory, those paired with their preferred male would produce more sons (Charnov 1983; Frank 1990; Booksmythe et al. 2017). For example, the proportion of sons increases with the intensity of the sexual characters of the mate in barn swallows (Saino et al. 2002). In tits, brood sex-ratio has been related to male quality, with females producing more sons when paired with a high-quality male (Svensson and Nilsson 1996; Kölliker et al. 1999; Sheldon et al. 1999; Griffith et al. 2003; but see Limbourg et al. 2013). However, our female blue tits were significantly repeatable in their brood sex-ratio (see below), whatever the pairing treatment. They therefore did not produce more sons when paired with their preferred male, which does not support the sex-allocation theory. Consequently, none of the two hypotheses has been verified.

Females thus express preferences for certain males without adjusting their breeding decisions according to whether or not their pairing matched their preferences. One possibility is that females may have expressed a social, instead of a sexual preference in our preference testing. Females were indeed not fully photostimulated at the time of testing, and therefore not sexually active yet (Dawson et al. 2001). Stimulating females with long photoperiods, or exogenous oestradiol capsules, would have ensured sexual responses to males (Byers and Kroodsma 2009; Reparaz et al. 2014; Caro et al. 2021), but at the cost of interfering with the reproductive experiment that followed the preference testing. Furthermore, in the wild, tits are often seen in pairs as early as February (Caro, pers. obs.) and can be found roosting in nest-boxes close to the one in which they will reproduce much later in the season (Salis et al. 2019). Finally, using the same mate preference testing apparatus, we recently showed that the more time female great tits had spent close to the male with which they were then paired in aviaries, the earlier they reproduced (Delaitre et al. 2023). This strongly suggests that we effectively captured sexual preferences during the mate preference tests, and that our experimental set-up

cannot itself explain the absence of an effect of the female preferences on their reproductive decisions.

We must also remember that we used captive birds with unlimited food access. Consequently, environmental constraints might not be harsh enough for females to adapt reproductive decisions with respect to the quality of their mate the same way they would have done it in the wild. Captivity can however not be the only explanation for the results obtained here, given that among the studies described above to illustrate each of the hypotheses, many were similarly conducted in captivity (Burley 1981b; Balzer and Williams 1998; Gil et al. 1999; Bolund et al. 2009). In fact, another hypothesis seems to emerge from our results, supporting that female blue tits are consistent in their main reproductive decisions, whatever their preference for the male with which they are paired.

Males seem to play a minor role in the major breeding decisions in blue tits. Females were indeed consistent in several of their reproductive decisions across the two years, despite the fact that they were paired with males that were at the opposite ends of their preference rankings. We found relatively high repeatability for laying date, clutch size, egg size, and proportion of sons, suggesting that females were consistent whatever the pairing treatment to which they were assigned. For example, in 2021, females paired with their preferred male laid more eggs (Table 2). While this was totally in line with our initial hypothesis, in 2022, we found the opposite pattern, with more eggs laid in the group of females paired with the male they avoided most. Since we reversed the treatment for each female between the two years, each female was acting as its own control. Females that laid numerous eggs in 2021 with the preferred male were thus the same females that laid numerous eggs in 2022 with the avoided male. This result was confirmed by the significant repeatability of laying dates and clutch sizes within females. This accessorially also shows the importance of repeating experiments over multiple years to avoid confounding effects of unidentified environmental variables, which in our case seem to be that the preferred group of 2021 contained females investing more in reproduction, regardless of the treatment applied to these females. There are other passerine species, like the collared flycatcher (*Ficedula albicollis*) (Sheldon et al. 2003) or the European starlings (*Sturnus vulgaris*) (Cornell et al. 2017), in which male quality does not influence female laying dates or clutch sizes. In zebra finches, a study found no evidence of a difference in reproductive timing and investment between females that were force-paired and those that were free to choose their partner (Griffith et al. 2017). Earlier studies on blue tit populations from the Mediterranean region have shown that males play little role in reproductive phenology. In Corsica, male blue tits from two distinct populations indeed start developing their

reproductive system at the same time in late winter, despite the fact that their females lay more than one month apart (Caro et al. 2005; Caro et al. 2006). Further quantitative genetic analyses revealed that the timing of breeding was solely driven by the females, with no evidence for an additive genetic male effect on laying dates (Caro et al. 2009). Finally, reproductive experiments crossing males and females from different populations suggested that the timing of laying matched the origin of the females and not the origin of the males (Caro et al. 2007). Interestingly however, although there is evidence for a higher heritability and repeatability of laying dates in female than male great tits (van Noordwijk et al. 1981; Van Der Jeugd and McCleery 2002; Noordwijk et al. 2002), we recently found that female great tits paired with a male they preferred during a preference test laid their first clutch earlier (Delaitre et al. 2023). Contrary to the present study however, all those female great tits were paired with one of their favorite males, and none with the male they avoided most. In any case, our results highlight the fact that female investment in reproduction might be species, and potentially even population-specific.

To conclude, this study suggests that although females have expressed preferences for some ornamental traits in males, based in part on their own phenotype, the male with which they are paired does not alter their reproductive decisions. The fact that females lead most reproductive decisions has already been shown in earlier studies in the wild on Mediterranean blue tits (Caro et al., 2007; 2009). In this species, males might thus be primarily used for providing genes and for helping rearing offspring. Consequently, females breeding with a male that does not match their selection criteria, either because their preferred male was already mated with another female, or because they only encounter less-preferred males, will not prevent them from breeding. This could be an adaptive strategy in such a short-living bird that, on average, has only two breeding seasons over its lifetime (Olioso 2017).

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Supplementary material

Whoever their partner, female blue tits breed the same.

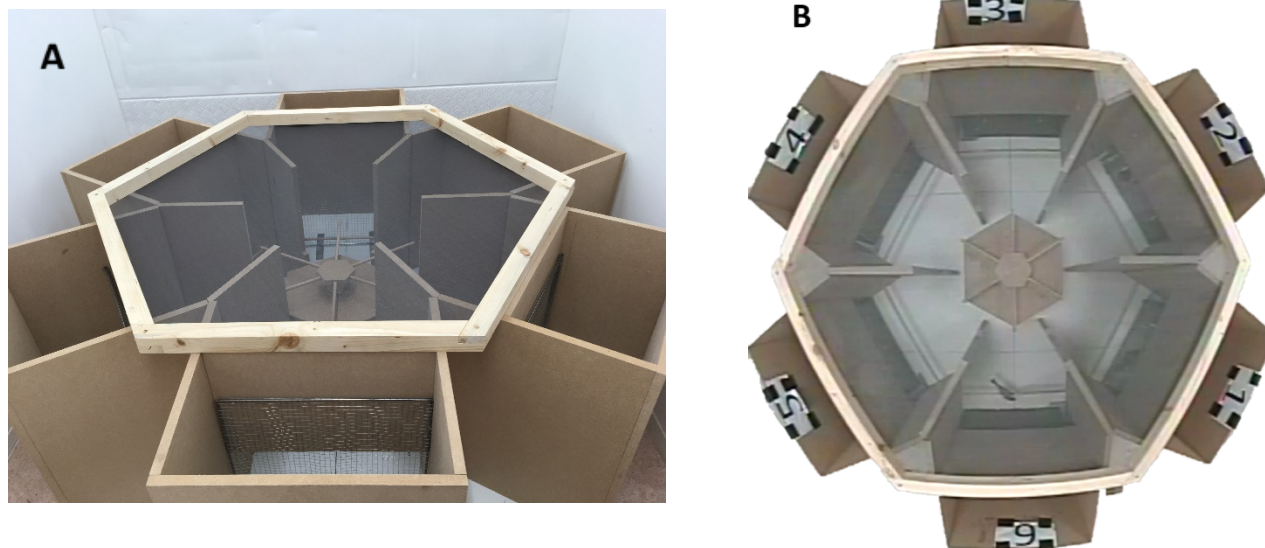


Figure S1: Pictures of the experimental setup for the mate preference test.

A: Picture of the carousel-shaped six-choice chamber. The roof can be moved to introduce the female into the setup.

B: Screenshot of the video of a test, the female is in the choice zone of the male 6. The males are not visible on the video.

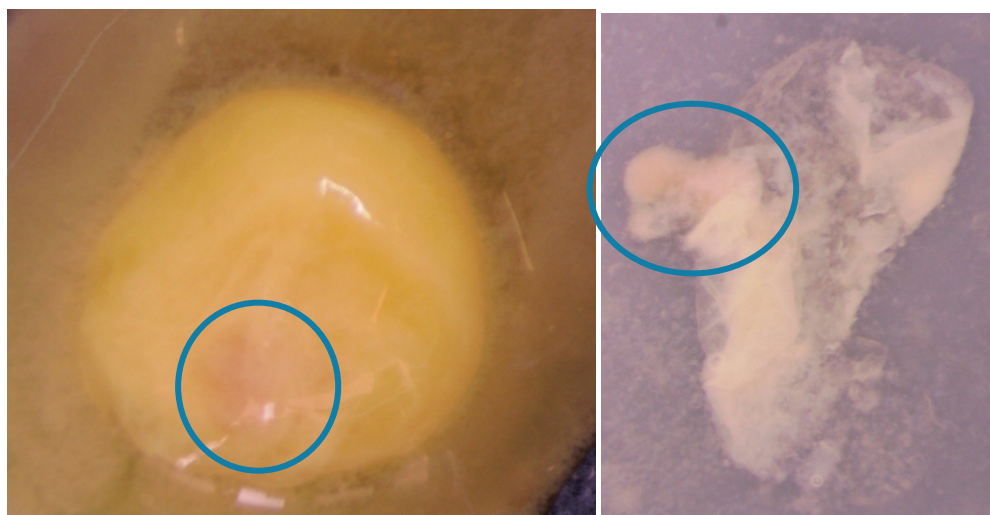


Figure S2: Fertile germinal disc (GD) showing an early stage developed embryo (circle).

Embryos that have died at early stages of development cannot be identified by simply candling the egg. This can be done by opening the egg and analysing the germinal disc. For more information on the procedure, see: <https://www.zsl.org/science/bringing-threatened-species-back-from-the-brink-of-extinction/practical-resources-for>.

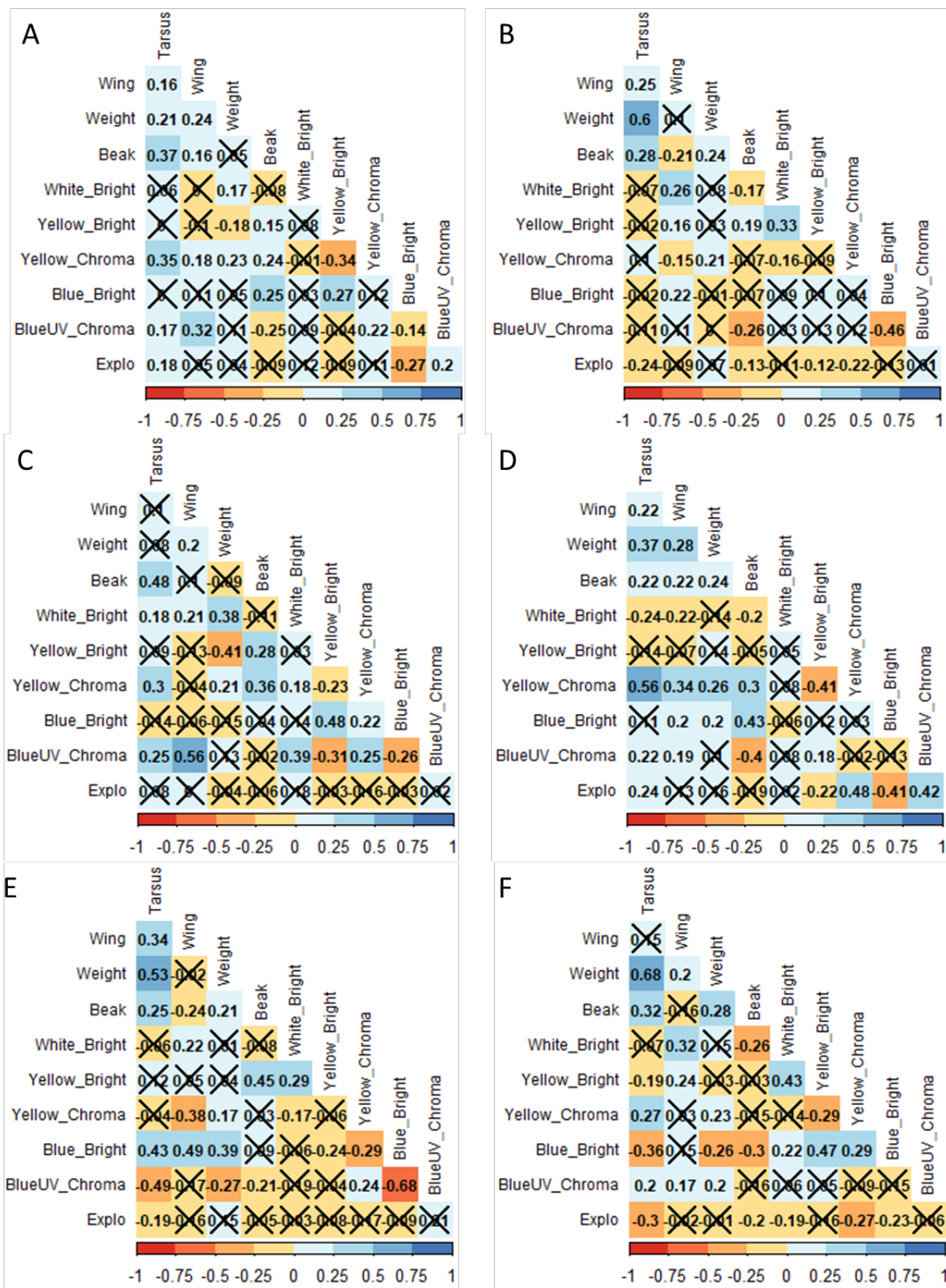


Figure S3: Correlation matrix of the traits of male and females.

A: Correlation of male traits for 2021 and 2022 together

B: Correlation of female traits for 2021 and 2022 together

C: Correlation of male traits for 2021

D: Correlation of male traits for 2022

E: Correlation of female traits for 2021

F: Correlation of female traits for 2022

Number in the coloured square are the Pearson correlation coefficients. Non-significant correlation ($p > 0.05$) are crossed out.

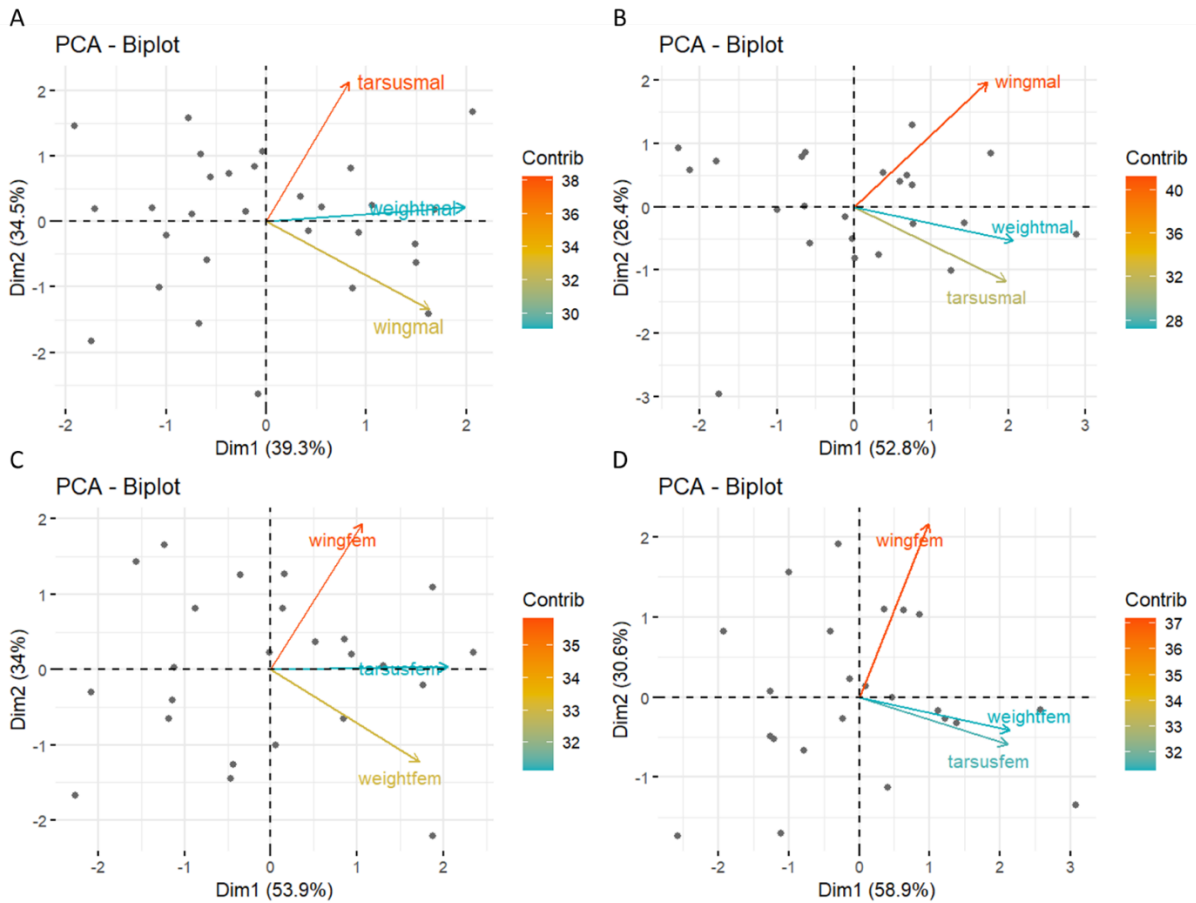


Figure S4: Biplot of the PCA ran for body size.

A: 2021 for males

B: 2022 for males

C: 2021 for females

D: 2022 for females

Each point depicts an individual.

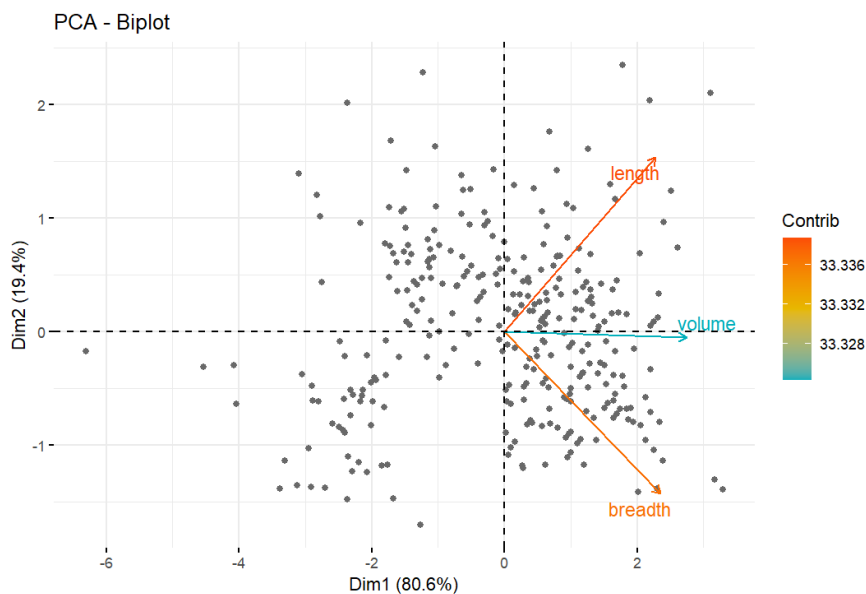


Figure S5: Biplot of the PCA ran for egg size. (n = 320)

High value of the first axis represents bigger eggs.